Year: 2012

Response to Comments on "Productivity Is a Poor Predictor of Plant Species Richness"

Grace, J B ; Adler, P B ; Seabloom, E W ; Borer, E T ; Hillebrand, H ; Hautier, Y ; Hector, A ; Harpole, W S ; O'Halloran, L R ; Anderson, T M ; Bakker, J D ; Brown, C S ; Buckley, Y M ; Collins, S L ; Cottingham, K L ; Crawley, M J ; Damschen, E I ; Davies, K F ; DeCrappeo, N M ; Fay, P A ; Firn, J ; Gruner, D S ; Hagenah, N ; Jin, V L ; Kirkman, K P ; Knops, J M H ; La Pierre, K J ; Lambrinos, J G ; Melbourne, B A ; Mitchell, C E ; Moore, J L ; Morgan, J W ; Orrock, J L ; Prober, S M ; Stevens, C J ; Wragg, P D ; Yang, L H

Abstract: Pan et al. claim that the results by Adler et al. actually show a strong linear positive relationship between productivity and richness, while Fridley et al. contend that the data show a strong humped relationship. These responses illustrate how the preoccupation with bivariate patterns distracts from a deeper understanding of the multivariate mechanisms that control these important ecosystem properties.

DOI: https://doi.org/10.1126/science.1214939

Originally published at:
Grace, J B; Adler, P B; Seabloom, E W; Borer, E T; Hillebrand, H; Hautier, Y; Hector, A; Harpole, W S; O'Halloran, L R; Anderson, T M; Bakker, J D; Brown, C S; Buckley, Y M; Collins, S L; Cottingham, K L; Crawley, M J; Damschen, E I; Davies, K F; DeCrappeo, N M; Fay, P A; Firn, J; Gruner, D S; Hagenah, N; Jin, V L; Kirkman, K P; Knops, J M H; La Pierre, K J; Lambrinos, J G; Melbourne, B A; Mitchell, C E; Moore, J L; Morgan, J W; Orrock, J L; Prober, S M; Stevens, C J; Wragg, P D; Yang, L H (2012). Response to Comments on "Productivity Is a Poor Predictor of Plant Species Richness". Science, 335(6075):1441.
DOI: https://doi.org/10.1126/science.1214939

Response to Comments on "Productivity Is a Poor Predictor of Plant Species Richness": Towards a Multivariate Representation of the Multiple Mechanisms Controlling Productivity and Diversity

James B. Grace[1*], Peter B. Adler[2], Eric W. Seabloom[3], Elizabeth T. Borer[3], Helmut Hillebrand[4], Yann Hautier[5], Andy Hector[5,6], W. Stanley Harpole[7] , Lydia R. O'Halloran[8], T. Michael Anderson[9], Jonathan D. Bakker[10], Cynthia S. Brown[11], Yvonne M. Buckley[12], Scott L. Collins[13], Kathryn L. Cottingham[14], Michael J. Crawley[15], Ellen I. Damschen[16], Kendi F. Davies[17], Philip A. Fay[18], Jennifer Firn[19], Daniel S. Gruner[20], Nicole Hagenah[21,22], Virginia L. Jin[23], Kevin P. Kirkman[21], Johannes M. H. Knops[24], Kimberly J. La Pierre[21], John G. Lambrinos[25], Brett A. Melbourne[17], Charles E. Mitchell[26], Joslin L. Moore[27], John W. Morgan[28], John L. Orrock[16], Suzanne M. Prober[29], Carly J. Stevens[30], Peter D. Wragg[3], Louie H. Yang[31]

[1]US Geological Survey, National Wetlands Research Center, 700 Cajundome Blvd., Lafayette, LA, 70506, USA, [2]Department of Wildland Resources and the Ecology Center, Utah State University, 5230 Old Main, Logan, UT, 84322, USA. [3]Ecology, Evolution, and Behavior, University of Minnesota, 1987 Upper Buford Circle, St. Paul, MN, 55108, USA. [4]Institute for Chemistry and Biology of the Marine Environment, University of Oldenburg, Schleusenstrasse 1, Wilhelmshaven, D-26381, Germany. [5]Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, Zurich, 8057, Switzerland. [6]Microsoft Research, Cambridge, UK. [7]Ecology, Evolution and Organismal Biology, Iowa State University, 133 Bessey Hall, Ames, IA, 50011, USA. [8]Department of Zoology, Oregon State University, 3029 Cordley Hall, Corvallis, OR 97331, USA. [9]Department of Biology, 206 Winston Hall, Wake Forest University, Box 7325 Reynolda Station, Winston-Salem, NC, 27109, USA. [10]School of Forest Resources, Box 354115, University of Washington, Seattle, WA, 98195-4115, USA. [11]Bioagricultural Sciences and Pest Management, Colorado State University, 1177 Campus Delivery, Fort Collins, CO, 80523-1177, USA. [12]School of Biological Sciences, The University of Queensland, St. Lucia, Queensland, 4072, Australia. [13]Department of Biology, MSC03-2020, University of New Mexico, Albuquerque, NM, 87131, USA. [14]Biological Sciences, 6044 Gilman Laboratory, Dartmouth College, Hanover, NH, 3755, USA. [15]Department of Biological Sciences, Imperial College London, Silwood Park, Ascot, Berks, SL5 7PY, UK. [16]Department

of Zoology, University of Wisconsin, 250 N. Mills Street, Madison, WI, 53704, USA.[17]Ecology and Evolutionary Biology, RL-1 120, University of Colorado, 1560 30th St, Boulder, CO, 80309, USA. [18]Grassland Soil and Water Research Lab, USDA ARS , 808 E Blackland Rd, Temple, TX, 76502, USA. [19]Queensland University of Technology, School of Biogeosciences, Brisbane QLD, 4001 Australia. [20]Department of Entomology, University of Maryland, College Park, 4112 Plant Sciences, College Park, MD, 20742, USA. [21]School of Biological and Conservation Sciences, University of KwaZulu-Natal, Pietermaritzburg, KwaZulu-Natal, 3209, South Africa. [22]Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT, 06520, USA, [23]Agroecosystem Management Research Unit, 137 Keim Hall, USDA ARS, Lincoln, NE, 68583- 0937, USA. [24]School of Biological Sciences, 348 Manter Hall, University of Nebraska, Lincoln, NE, 68588, USA. [25]Department of Horticulture, Oregon State University, 4017 Ag and Life Sciences Building, Corvallis, OR, 97331, USA. [26]Department of Biology, 411 Coker Hall, University of North Carolina at Chapel Hill, Chapel Hill, NC, 27599-3280, USA. [27]School of Botany, University of Melbourne, Parkville, Victoria, 3010, Australia. [28]Department of Botany, La Trobe University, Bundoora, Victoria, 3086, Australia. [29]CSIRO Ecosystem Sciences, Private Bag 5, Wembley, Western Australia, 6913, Australia. [30]Department of Life Sciences, The Open University, Walton Hall, Milton Keynes, Buckinghamshire, MK7 6AA, UK and Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, UK. [31]Department of Entomology, University of California, Davis, One Shields Avenue, Davis, CA, 95616, USA.

*To whom correspondence should be addressed. E-mail: gracej@usgs.gov

Pan et al. claim that the results by Adler et al. actually show a strong linear positive relationship between productivity and richness, while Fridley et al. contend that the data show a strong humped relationship. These responses illustrate how the preoccupation with bivariate patterns distracts from a deeper understanding of the multivariate mechanisms that control these important ecosystem properties.

Debate over the productivity-richness relationship (PRR) has been strongly influenced by the way that scientific motives influence how theories are evaluated. Analyses of how scientists participate in the process of theory maturation (*1*) point out that attachment to particular explanations can result in a tendency to overlook inadequacies and contradictions. Such attachment can lead to a reliance on "theory demonstrations," which selectively sift through data to find supporting evidence. "Theory investigations," in contrast, have a different motivation – to evaluate the explanatory adequacy and limitations of theories so as to improve them. Theory investigations are challenged to be either exhaustive in their examination of evidence (e.g., through complete meta-analyses) or to rely on unfiltered samples that represent the variation nature has to offer. Generally, demonstrations seek qualitative (yes/no) support while theory investigations seek to quantify relative importances of different processes.

In our investigation of the PRR, we examined patterns at the local, regional, and global scale (*2*). In addition, we considered and reported the patterns one could find if they included all sites or if one excluded sites that were disturbed. In addition to analyzing mean responses, we additionally evaluated boundaries using nonlinear quartile regression methods. We summarized and reported the findings from many different analyses of the data. We noted that for all of the analyses conducted, that there was a great deal of unexplained variance.

Pan et al. (*3*) argue that our study provides clear and strong support for a positive linear relationship between productivity and richness. They selected our subset analysis where we found a weak, positive linear PRR among site means (the straight dotted line in Adler et al., Fig. 3), further culled sites from that subset, and then averaged across similar sites, boosting the apparent strength of the relationship. Pan et al. (*3*) claim that we were biased in our investigation of the PRR because of unbalanced replication of samples across the bins in the community classification scheme they used to post-process the data. Counter to their claim, there is no requirement for equal representation in bins unless one seeks homogeneity of variance across the relationship. Averaging across similar sites so as to create a single value for each bin, however, reduces unexplained variance by eliminating within-bin variance and exaggerates predictive capacity. The use of bins defined by an informal community classification scheme also confounds productivity with the classification scheme.

In sharp contrast to Pan et al., Fridley et al. (*4*) contend that our data show strong support for the Humped-Back Model (HBM). Original support for the HBM comes from theory demonstrations, such as the Al-Mufti (*5*) study where data were hand-selected to represent a humped-back line. Theory investigations based on unfiltered samples and rigorous quantitative analyses since that time have consistently found PRR patterns to be weak and variable (*6*, *7, 8*), consistent with our findings (though analyses that have filtered studies have produced more consistent results, with the form of relationship depending on the filter used, *9*, *10*).

Fridley et al.'s specific claims are that we 1) filtered data by eliminating anthropogenic sites, 2) failed to properly test the "humped-back model" HBM by not including litter, 3) failed to include enough high-productivity sites to detect a hump, and, inconsistent with that point, 4) claim the data show a humped relationship. We dispute their implication that we presented biased results and disagree with their conclusions as described here :

1) We performed many analyses and summarized the full range of patterns found. One of the analyses prominently presented was across all sites (Adler et al. Fig. 3, solid line), and showed a weak but significant humped relationship. Another analysis excluded anthropogenic sites (Adler et al. Fig. 3, dotted line) anticipating that some might object to inclusion of highly altered sites (which Pan et al. did). This analysis showed a

(weak) linear positive relationship. Within-site analyses of small-scale richness patterns showed very weak and highly various patterns (Adler et al. Fig. 2).

2) The majority of studies of the PRR have described productivity as the variable of theoretical interest rather than accumulated biomass, including Fridley et al. themselves at times (*9*, p. 127). To be comparable with previous theory investigations, we analyzed productivity without including litter accumulated from previous years.

3) Sites were selected without filtering and represent the variance encountered when ecologists are asked to sample natural grasslands. Selectively including sites with high productivity as suggested by Fridley et al. would bias the sample, leaving us with no estimate of the predictive adequacy of the PRR. That said, 20 of the 48 sites included in our study reported plot productivity levels greater than 500 g/m^2 and 8 had levels greater than 800 g/m^2 (and ranged over 1,500 g/m2), counter to the impression given by Fridley et al.

4) Fridley et al. suggest, based on visual examination and no formal analysis, that there is a clear modal PRR relationship, contradicting their own claim that more high productivity sites are needed to detect a humped relationship. However, production and richness data are lognormal variables (Adler et al. Fig 2) and a random bivariate sample from a lognormal distribution will necessarily have a humped appearance in linear space (Fig. 1A). Plotting data from a bivariate lognormal distribution in log-log space (Fig. 1B) reveals the randomness. The observed data (Fig. 1C and 1D) show only modest deviations from random expectations, illustrating why quantitative analyses failed to detect strong patterns.

We note that even if productivity and richness were strongly correlated, we still would be unable to resolve underlying mechanisms. There have been well over 100 theories proposed to explain diversity patterns (*11*). A linear positive relationship is predicted by many different possible mechanisms (*12*) while the HBM likewise represents a large collection of conflicting theories (*7*).

We reiterate that it is past time to develop the multivariate expectations for our multiprocess theories and evaluate those expectations quantitatively (*13*). Insights into the mechanisms controlling diversity cannot be achieved by continued fixation on bivariate patterns such as the PRR.

References and Notes

1. C. Loehle, *Quarterly Review of Biology* **62**, 397 (1987).
2. P. B. Adler *et al.*, *Science* **333**, 1750 (2011).
3. X. Pan, F. Liu, M. Zhang, Science (submitted)
4. J. D. Fridley, *et al.*, *Science* (submitted).
5. M. M. Al-Mufti, C. L. Sydes, S. B. Furness, J. P. Grime, S. R. Band, *Journal of Ecology* **65**, 759 (1977).
6. Mittelbach, G.G., et al. Ecology, **82**, 2381–2396 (2001).
7. J. B. Grace, Perspectives in Plant Ecology, Evolution, and Systematics 2, 1-28 (1999).
8. Gross, K.L., Willig, M.R., Gough, L., Inouye, R. & Cox, S.B. Oikos **89**, 417–427 (2000).
9. M. A. Huston, *Biological Diversity* (Cambridge Univ. Press, UK, 1994)
10. L. N. Gillman, S. D. Wright, *Ecology* **87**, 1234 (2006).
11. M. W. Palmer, *Folia Geobotanica & Phytotaxonomica* **29**, 511 (1994).
12. Carnicer, J., L. Brotons, D. Sol, and M. de Caceres. Global Ecology and Biogeography **17**, 352-362 (2008)
13. J. B. Grace, Structural Equation Modeling and Natural Systems, Chapter 12 (Cambridge University Press, UK, 2006).

Figure Caption:

Figure 1. (A) Random expectations for plot-level data based on data characteristics in Adler et al. (*6*, Fig. 2). Note apparent hump produced by lognormal distributions of both biomass and species richness. (B) Random expectations for Adler et al. data in log-log space. (C) Observed data in linear space. (D) Observed data in log space.

Figure 1.